PALAEOBIOLOGY AND SYSTEMATICS OF LARGE CYCLOSTOME BRYOZOANS FROM THE PLIOCENE CORALLINE CRAG OF SUFFOLK

by PETER S. BALSON *and* PAUL D. TAYLOR

ABSTRACT. Bioclastic sands of the Coralline Crag are characterized by abundant bryozoans including large colonies of four cyclostomes: *Blumenbachium globosum* Koenig, *Meandropora aurantium* (Milne Edwards in Lyell), *M. tubipora* (Busk), and *Multifascigera debenensis* sp. nov. These species are systematically described and the relationships investigated between colony growth pattern, form, and inferred ecology. Colonies of each species are composed of numerous subcolonies bounded by exterior walls. Times of autonomous subcolony growth were punctuated by periods of subcolony anastomosis. Most colonies acquired a roughly hemispherical shape but others developed a subspheroidal form. The former apparently retained a stable attitude during growth whereas the latter either enveloped an unstable substrate (circumrotatory growth) or were attached to a perishable substrate which supported the colony above the sea-bed. Colonies are absent from the turbulent sandwave facies of the Coralline Crag but are present in other facies where mobile animals rather than currents may have been responsible for overturning circumrotatory colonies. Evolution of exterior wall-bounded subcolonies, known in many post-Palaeozoic cyclostomes, was possible because interzooidal pores allowed soft tissue connection between subcolonies beneath the colony surface when soft tissue was absent above it. The localization of coelomic damage may have been a factor in the success of this type of organization.

THE Coralline Crag is a marine Pliocene formation of bioclastic sands and silty sands which has a small outcrop in south-east Suffolk. The Coralline Crag and overlying Plio-Pleistocene Red Crag were originally considered to be parts of a single deposit but in 1835 Charlesworth showed that this was clearly divisible into two. The upper deposit he termed Red Crag after its distinctive coloration because of post-depositional staining by iron oxides. The lower deposit he termed Coralline Crag after the abundance of 'corals', later shown to be the skeletal remains of bryozoans (Wood 1844; Busk 1859). Among the most conspicuous of these bryozoans are the large colonies of four superficially similar species of cyclostome: *Blumenbachium globosum* Koenig, *Meandropora aurantium* (Milne Edwards in Lyell), *M. tubipora* (Busk) and *Multifascigera debenensis* sp. nov. The aim of this paper is to revise the systematics of these species and to explore the relationships between colony growth pattern, form, and inferred palaeoecology. Unless otherwise stated, specimens are held in the palaeontological collections of the British Museum (Natural History).

SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder CERIOPORINA Hagenow, 1851
Family incertae sedis
Genus BLUMENBACHIUM Koenig, 1825

Type species. Blumenbachium globosum Koenig, 1825, by monotypy.

Emended diagnosis. Colony composed of numerous stacked layers of cup-shaped subcolonies

bounded by exterior walls; subcolonies are free proximally but contiguous distally where exterior walls of adjacent subcolonies interdigitate.

Remarks. *Blumenbachium* Koenig, 1825 and *Alveolaria* Busk, 1859 have the same type species. Therefore, *Alveolaria* is an objective junior synonym of *Blumenbachium*. The only species of *Blumenbachium* which has been described is *B. globosum* from the Coralline Crag. Lonsdale in Murchison (1839) and d'Orbigny (1850) used *Blumenbachium* incorrectly when referring to small discoidal bryozoans of Silurian age.

Familial assignment of *Blumenbachium* remains in doubt and, indeed, its subordinal assignment to the Cerioporina must be considered tentative until the cerioporinids as a group are better understood.

Blumenbachium globosum Koenig, 1825

Plate 55, figs. 5, 6; Plate 56, figs. 1, 3, 4; text-figs. 1, 2, 5, 7, 8

1825 *Blumenbachium globosum* Koenig, p. 3, pl. 5, fig. 69.
?1844 *Theonoa*(?) *globosa* Wood, p. 13.
1859 *Alveolaria semiovata* Busk, p. 128, pl. 19, fig. 4; pl. 21, fig. 3.
1889 *Alveolaria semiovata* Busk; Nicholson and Lydekker, p. 620, fig. 463.
1922 *Alveolaria semiovata* Busk; Canu and Bassler, p. 111, fig. 32, pl. 18, figs. 1–4.
1948 *Alveolaria semiovata* Busk; Chatwin, fig. 17, 12.
1952 *Alveolaria semiovata* Busk; Lagaaij, p. 185, pl. 26, fig. 2.
1953 *Alveolaria semiovata* Busk; Bassler, p. G70, fig. 35, 5.
1957 *Alveolaria semiovata* Busk; Buge, p. 116, pl. 5, fig. 6.

Lectotype. D 52755 'White Crag, Suffolk'. C. Koenig Collection. Figured by Koenig (1825, pl. 5, fig. 69 lower colony).

Paralectotype. D 52754 'White Crag, Suffolk'. C. Koenig Collection. Figured by Koenig (1825, pl. 5, fig. 69 upper colony).

Other material. Coralline Crag, Suffolk: 8814, 23474, 51157, 60209, 60479, B 1385 (described by Smith 1817), B 1704, B 1712, B 4290, B 4308, B 4311, D 1495, D 6902–4, D 6905 (lectotype of *Alveolaria semiovata* Busk, 1859 chosen by Lagaaij 1952), D 51067–70, D 52767–8, D 52773–4, D 53128–31, Sedgwick Museum (Cambridge) C 50972.

Description. Colonies vary in shape from roughly spheroidal (Pl. 56, fig. 1) to hemispherical (Pl. 55, fig. 6), and are composed of numerous radially arranged subcolonies, each bounded laterally by an exterior wall. Subcolonies are free proximally but are contiguous and generally six-sided distally where their bounding exterior walls are convoluted and interdigitate with those of adjacent subcolonies (text-fig. 5). The united edges of adjacent subcolonies stand out as ridges, bisected by the protuberant juxtaposed exterior walls, forming a polygonal network on the zoarial surface (text-fig. 7). New generations of subcolonies arise from the surface of earlier subcolonies. In section, colonies are concentrically layered, each layer consisting of a single generation of united subcolonies (text-fig. 8).

Zooecia were budded by division of existing interzooecial walls on subcolony-bounding exterior walls (acting as budding laminae), and interzooecially (see McKinney 1975) by interzooecial wall division at triple junctions between established zooecia. Zooecia are tubular and polygonal in cross-section. They are occasionally divided by one or more subterminal diaphragms (see Nye 1968), convex distally (text-fig. 1), and sometimes
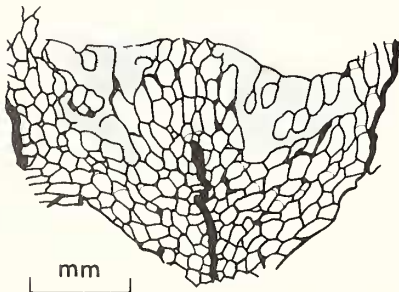
TEXT-FIG. 1. *Blumenbachium globosum* Koenig, D 6905. Drawing of a thin section through a brood chamber (stippled). Pendant-like structures (right of centre) are autozooecia supported within the chamber by interior walls. Curved walls projecting into chamber (left of centre) may be interior walls partially resorbed during brood chamber formation. Thin, convex upwards walls partitioning some autozooecia are interpreted as subterminal diaphragms.

mm

closed by a terminal diaphragm. The polygonal apertures of mature zooecia average about 0·11 mm in width. Distinction between autozooecia and any kenozooecia is unclear although some colony surfaces exhibit longitudinal rows of relatively large, slightly protuberant, open zooecia (probably autozooecia) separated from one another by rows of smaller zooecia (possibly kenozooecia) which are characteristically occluded by convex diaphragms. Structures resembling lunaria occur in a few colonies. Brood chambers are rare but when present are extensive and occupy the depressed centre of the cup-shaped subcolonies. The roof of the brood chamber is a thin ?exterior wall pierced by scattered autozooecia, typically occluded by terminal diaphragms (text-fig. 2A). Together with interior walls, these zooecia divide the brood chamber internally (text-fig. 1). Ooeciopores have not been positively identified.

Remarks. This species is often referred to as *Alveolaria semiovata* Busk, 1859, but Koenig's first description of *Blumenbachium globosum* in 1825 predates that of *Alveolaria semiovata*. The name *Blumenbachium globosum* was later used by Prestwich (1871, p. 123) and is here revived for this common Coralline Crag fossil. A lectotype (Pl. 56, fig. 1) and a paralectotype have been chosen from Koenig's syntypes which clearly match his illustrations.

Prior to Koenig's publication, Sowerby (1804–1817) figured *B. globosum* (pl. 481, lower figure) describing it as 'a sort of *Millepora*'. The first of the unnamed Crag 'zoophytes' described by William Smith (1817) is also *B. globosum* (specimen B 1385), as is the bryozoan illustrated by R. C. Taylor (1830, fig. 65*a*, *b*) also described as a 'crag zoophyte'.

Stratigraphical occurrence. Pliocene: Coralline Crag (Gedgravian) of Suffolk, England; Scaldisian of the Scheldt Estuary, Holland (Lagaaij 1952); Redonian of Saint-Denis-d'Oleron, France (Buge 1957).

B. globosum also occurs as a derived fossil in Plio-Pleistocene deposits, notably the Red Crag of East Anglia.
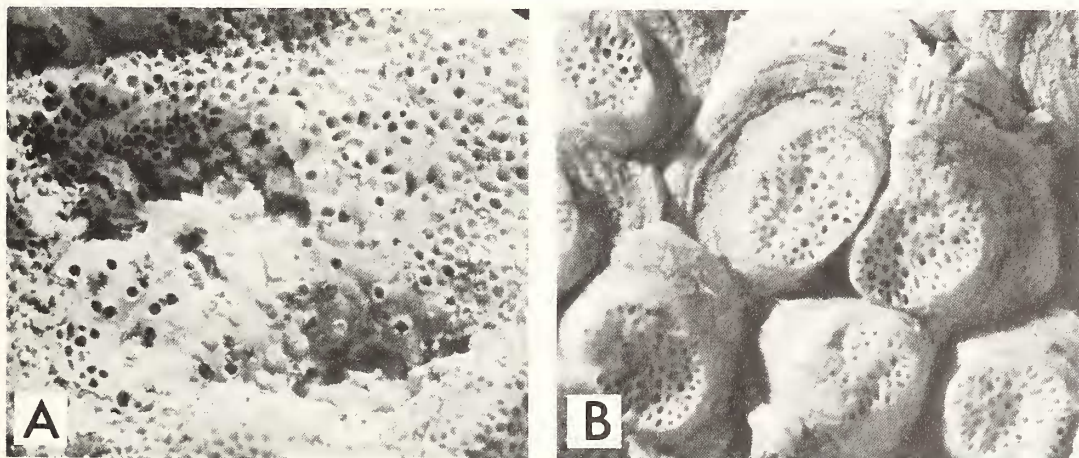
<div align="center">

Suborder TUBULOPORINA Milne Edwards, 1838
Family FRONDIPORIDAE Busk, 1875
Genus MEANDROPORA d'Orbigny, 1849

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Type species. Fascicularia aurantium Milne Edwards *in* Lyell 1838.

Emended diagnosis. Frondiporidae with large colonies composed of radiating, cylindrical fascicles of elongate zooids which divide and anastomose at intervals.

TEXT-FIG. 2. *Blumenbachium globosum* Koenig. A, surface of a brood chamber pierced by circular autozooecial apertures some of which are occluded, B 1704, Coralline Crag, Sutton, × 13. B, cup-shaped subcolonies on the underside of a fractured specimen, D 1495, Coralline Crag, Suffolk, × 12.

Remarks. Meandropora was established by d'Orbigny in 1849 to replace the *Fascicularia* of Milne Edwards (in Lyell 1838) which is not the same as that of Lamarck (1812). Three species of *Meandropora* are generally recognized: *M. aurantium* (Milne Edwards in Lyell 1838), given as the type species by d'Orbigny (1849), *M. tubipora* (Busk 1859), and *M. cerebriformis* (de Blainville 1830). The first two species occur in the Coralline Crag and are described below. *M. cerebriformis* is characterized by a meandroid pattern of fascicles on the colony surface (see Buge 1948, pl. 7, figs. 3–4).

Meandropora aurantium (Milne Edwards in Lyell, 1838)

Plate 54, figs. 5, 6; Plate 55, fig. 1; Plate 56, figs. 2, 6, 7

1838	*Fascicularia aurantium* Milne Edwards [sp. nov.]; Lyell, p. 303, fig. 133.
1844	*Fascicularia aurantium* Milne Edwards; Wood, p. 13.
1859	*Fascicularia aurantium* Milne Edwards; Busk, p. 131, pl. 21, fig. 3.
1890	*Fascicularia aurantium* Milne Edwards; Reid, fig. 3.
1948	*Theonoa aurantium* (Milne Edwards); Chatwin, fig. 17, 10.
1952	*Meandropora aurantium* (Milne Edwards); Lagaaij, p. 178, pl. 23, fig. 4.
1957	*Meandropora aurantium* (Milne Edwards); Buge, p. 102, pl. 5, figs. 3, 4.
?1963	*Meandropora aurantium* (Milne Edwards); Malecki, p. 79, pl. 8, fig. 10.

Type. The location of the figured type specimen is unknown and it may be lost. However, as the identity of the species is in no doubt, circumstances do not warrant the designation of a neotype.

Material. Coralline Crag, Suffolk: 8792, 8802, 8812–13, 8845–8, 40034, B 1384 (described by Smith 1817), B 1664, B 3828, B 4294, B 4306, B 4311, D 2079, D 6671, D 6906, D 52765–6, D 52769, D 52775, Sedgwick Museum (Cambridge) C 51082, C 51085.

Emended diagnosis. Meandropora with fascicles of subcircular cross-section, generally dividing and anastomosing at irregular intervals.

Description. Colonies are spheroidal (Pl. 56, fig. 2) subspheroidal, or hemispherical (Pl. 56, fig. 6) and composed of numerous radially arranged, elongate fascicles of zooecia subcircular in cross-section. Their bounding exterior walls may be ornamented by the longitudinal traces of interzooecial walls and occasional growth lines transverse to fascicle length. Division and anastomosis of fascicles generally occurs at irregular intervals, although phases of extensive fascicle anastomosis in some colonies gives rise to solid concentric bands of zooecia (Pl. 56, figs. 6, 7) with little interfascicular space (Pl. 54, fig. 5).

Zooecia open at the distal ends of fascicles (Pl. 54, fig. 6) and were budded by interzooecial division (McKinney 1975) of existing walls within the axial regions of the fascicles. Termination of zooecia usually occurs where they meet the bounding wall of the fascicle after divergence from the centre of the fascicle. More rarely, groups of zooecia are capped by terminal diaphragms following fascicle anastomosis. Zooecia are very long (> 5 mm), thin-walled and polygonal in cross-section. Some zooecia are partitioned by thin diaphragms (?basal diaphragms of Nye 1968) which may be located at the same level in adjacent zooecia. Apertures of mature zooecia average about 0·24 mm in width. Kenozooecia are not evident.

EXPLANATION OF PLATE 54

Figs. 1–2. *Multifascigera debenensis* sp. nov. D 52760, holotype, Coralline Crag, Ramsholt Cliff. 1, typical appearance of colony surface with an inflated gonozooid (arrowed) between autozooidal fascicles, × 9. 2, single subcolony with stellate pattern of fascicles, × 12.

Figs. 3–4. *Meandropora tubipora* (Busk). 3, columnar fascicles arising from discontinuous platform composed of occluded ?kenozooids, D 46751, Coralline Crag, near Sudbourne, × 9. 4, broken ovicell (arrowed) extending between fascicles, D 53154, Coralline Crag, Broom Hill, × 9.

Figs. 5–6. *Meandropora aurantium* (Milne Edwards in Lyell). 5, anastomosed fascicles giving a high density of apertures on colony surface, B 4311, Coralline Crag, × 9. 6, inflated ovicell frontal wall (arrowed) and incomplete ovicells present within fascicles as large apertures, D 52769, Coralline Crag, Aldeburgh Hall, × 11.

PLATE 54
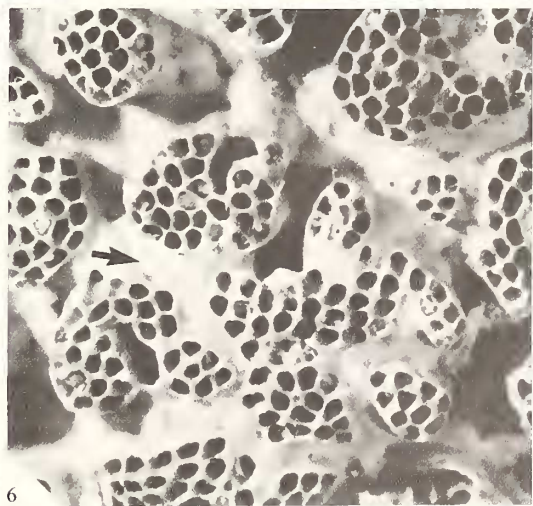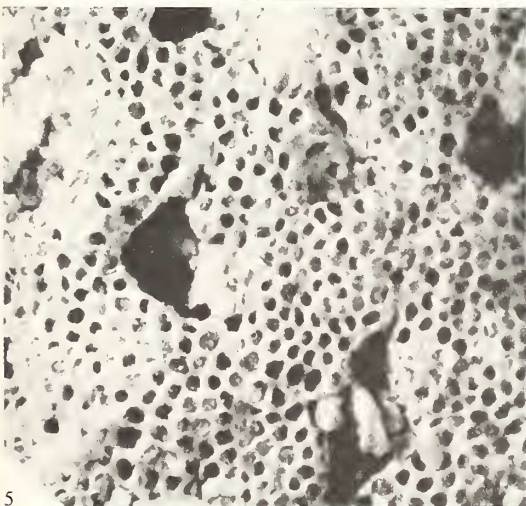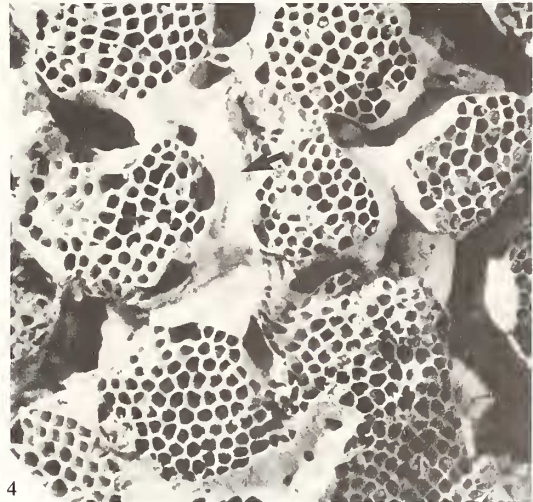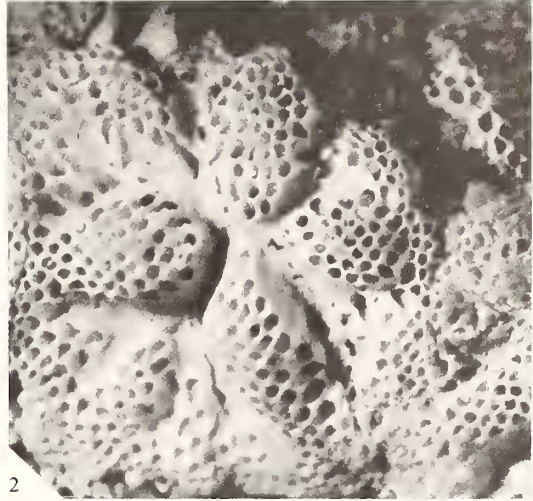
Ovicells occur in a small minority of colonies and are large chambers, possibly originating from a single zooecium, which span the gaps between adjacent fascicles and have thin roofs of exterior wall (Pl. 54, fig. 6). Fascicle diameter is diminished when ovicells are present. Occasional solitary zooecia, circular in cross-section, penetrate the ovicells and are usually occluded by terminal diaphragms. Ooeciopores are difficult to distinguish, although an occluded aperture (c. 0·11 mm in width and transversely elliptical) protruding through the frontal surface of one ovicell may be an ooeciopore.

Remarks. *Meandropora aurantium* was first named when figured as *Fascicularia aurantium* Milne Edwards by Lyell in his *Elements of Geology* (1838). Prior to this, the species was the second of two unnamed 'zoophytes' described by William Smith (1817). Chatwin (1948) incorrectly referred *M. aurantium* to the genus *Theonoa* (type species *T. chlatrata* Lamouroux from the Jurassic) which consists of small discoidal encrusting colonies with radiating linear fascicles of zooecia.

Stratigraphical occurrence. Pliocene: Coralline Crag (Gedgravian) of Suffolk, England; Scaldisian of Wilmars-donck, Holland (Lagaaij 1952); Redonian of Chalonnes and Sceaux-d'Anjou, Maine-et-Loire, France (Buge 1957). *M. aurantium* also occurs as a derived fossil in the Plio-Pleistocene Red Crag of East Anglia.

Meandropora tubipora (Busk, 1859)

Plate 54, figs. 3, 4; Plate 55, fig. 2; Plate 56, fig. 5

1859   *Fascicularia tubipora* (n. sp.); Busk, p. 130, pl. 21, fig. 1.
1859   *Fungella multifida* (n. sp.); Busk, p. 119, pl. 17, fig. 4.
?1887   *Fascicularia tubipora* Busk; Waters, p. 344.
1952   *Meandropora tubipora* (Busk); Lagaaij, p. 179, pl. 24, fig. 1.
1959   *Meandropora tubipora* (Busk); British Museum (Natural History), pl. 31, fig. 1.

Lectotype (here designated). B 4299 Coralline Crag, Suffolk. This is the specimen figured by Busk (1859) as pl. 21, fig. 1*b*.

Other material. Coralline Crag, Suffolk: 8799, 8801, 8814, 48711, 60207, 60478, B 1667, D 6679, D 46751, D 52770, D 52772, D 53133–4.

Emended diagnosis. *Meandropora* with fascicles which anastomose at regular intervals to form platforms transverse to colony growth direction.

Description. Hemispherical to spheroidal colonies composed of radiating fascicles of zooecia which anastomose with adjacent fascicles at regular intervals to form platforms (Pl. 55, fig. 2). New generations of fascicles arise from the platforms between areas composed of occluded zooecia (?kenozooecia); fascicles are subcircular in cross-section and have slightly domed distal growing surfaces. Exterior walls bounding fascicles are commonly ornamented by longitudinal traces of interzooecial walls and may bear faint growth lines.

EXPLANATION OF PLATE 55

Fig. 1. *Meandropora aurantium* (Milne Edwards in Lyell), colony with large basal hollow which may have served as a crab domicile, Sedgwick Museum C 51082, Coralline Crag, Broom pit, Gedgrave, × 0·75.
Fig. 2. *Meandropora tubipora* (Busk), fascicles with uniting platforms, D 52772, Coralline Crag, Aldeburgh Brick Works, × 3·7.
Figs. 3-4. *Multifascigera debenensis* sp. nov. Coralline Crag, Ramsholt Cliff. 3, large fractured colony, paratype, D 52761, × 0·6. 4, concentric layers of zooecial fascicles, holotype, D 52760, × 4.
Figs. 5-6. *Blumenbachium globosum* Koenig. 5, ridged colony surface with overgrowing cheilostomes (top and bottom right) and serpulid (right centre) which is gradually being covered by further bryozoan growth, D 52773, Coralline Crag, Crag Pit Nursery, × 5·5. 6, sectioned colony attached to a celleporid cheilostome itself encrusting a bivalve (represented by a mould, bottom right), D 52774, Coralline Crag, Aldeburgh Hall, × 0·9.

PLATE 55

BALSON and TAYLOR, Pliocene bryozoans
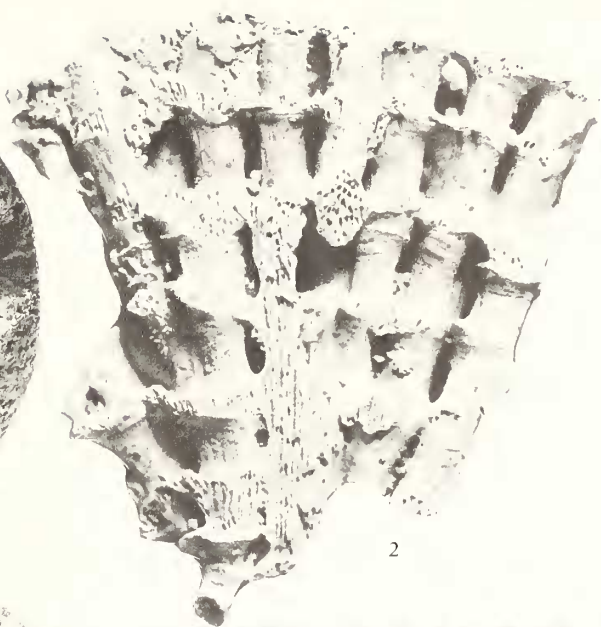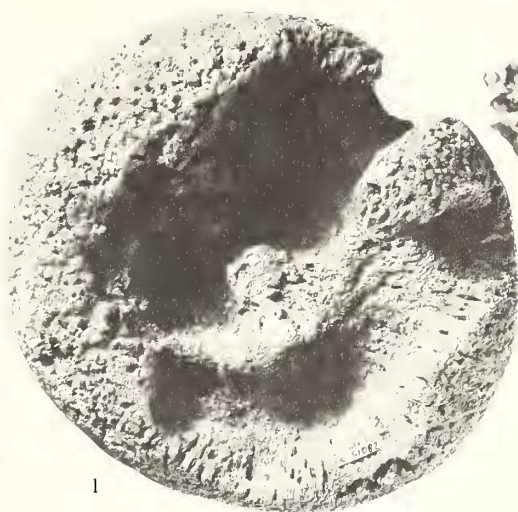
Zooecia are thin-walled and polygonal in cross-section (commonly six-sided) and were budded either interzooecially (McKinney 1975) within fascicles or on the budding lamina formed by the outwardly spreading exterior walls of anastomosing fascicles. Apertures of mature zooecia average about 0·20 mm in diameter. Inferred autozooecia forming the fascicles are very long. Possible kenozooecia (Pl. 54, fig. 3) forming the platforms between fascicles are short (< 1 mm) and are occluded by terminal diaphragms situated slightly beneath the level of the aperture.

Ovicells are uncommon and consist of extensive, irregular chambers (Pl. 54, fig. 4) attached to the exteriors of fascicles and seemingly arising from the platforms between fascicles. They may be partitioned by interior walls and penetrated by zooecia which support their thin pseudoporous roofs. Ooeciopores have not been positively identified.

Remarks. Busk's species *Fascicularia tubipora* was first referred to the genus *Meandropora* by Lagaaij (1952). Following an initial suggestion by Busk, Lagaaij considered *Fungella multifida* Busk, 1859 to be a juvenile stage of *Meandropora tubipora* and this opinion is adhered to here.

An unnamed 'zoophyte' illustrated by R. C. Taylor (1830, figs. 63, 64) is undoubtedly *M. tubipora*. Waters (1887) described a fossil which he referred to *M. tubipora* from the Pliocene of Napier, New Zealand. He also mentioned the occurrence of this species in the Pliocene of Ranetto, Sicily, and in Recent seas. However, these records have not been confirmed and, in the absence of illustrations, may be considered doubtful.

Although closely similar to *M. aurantium* in overall colony form, *M. tubipora* does differ in an aspect which would have been sufficient for Borg (1926, pp. 477–478) to have placed the two species in separate families. Borg considered fasciculate tubuloporinids with fascicles isolated by occlusion of zooecia between them (e.g. *M. tubipora*) to belong to the family Fasciculiporidae, and taxa with 'primary' fascicles (e.g. *M. aurantium*) to belong to the family Frondiporidae. The validity of this opinion cannot be assessed until cyclostome morphology is more clearly understood.

Stratigraphical occurrence. Pliocene: Coralline Crag (Gedgravian) of Suffolk, England.

Family THEONOIDAE Busk, 1859
Genus MULTIFASCIGERA d'Orbigny, 1853
Multifascigera debenensis sp. nov.

Plate 54, figs. 1, 2; Plate 55, figs. 3, 4

Derivation of name. The river Deben on whose banks the bryozoan is found.

Holotype. D 52760 Coralline Crag, Ramsholt Cliff (TM 298428), Suffolk.

Paratypes. D 52761–4 Coralline Crag, Ramsholt Cliff.

Diagnosis. Colony composed of numerous concentric layers of subcolonies united at their edges, each subcolony with a stellate pattern of zooecial fascicles; gonozooecia are interfascicular.

Description. Colonies are large, concentrically layered and tabular, hemispherical or spheroidal in shape (Pl. 55, fig. 3). Each concentric layer (Pl. 55, fig. 4) consists of numerous cup-shaped subcolonies united at their edges. Subcolonies are polygonal in plan view and have a stellate pattern of radiating fascicles on their upper surfaces (Pl. 54, fig. 2). Fascicles tend to have a rounded quadrate cross-sectional shape and their bounding exterior walls may be marked by longitudinal traces of interzooecial walls between slightly convex zooecia. Fascicles diverge obliquely upwards from the centre of the subcolonies and bend until their long axes become orientated almost at right angles to the layering of the colony. A minority of fascicles then expand outwards, overarching non-expanding fascicles, anastomosing with adjacent expanding fascicles, and forming a new concentric layer of subcolonies, each new subcolony being derived from a single expanding fascicle. Concentric wrinkles transverse to growth direction ornament the exterior wall on the undersides of subcolonies.

Zooecia open at the distal ends of fascicles. They were budded by division of interzooecial walls on the budding lamina of exterior wall forming the undersurface of the subcolonies. Zooecia are long, polygonal in cross-section, thin-walled (*c.* 0·01 mm) proximally (near the base of the subcolony), and thicker walled (*c.* 0·02 mm) distally (within the lengthening fascicle). Apertures of mature zooecia average about 0·16 mm in diameter.

Gonozooecia are rare, interfascicular, and apparently irregular in shape (Pl. 54, fig. 1). Ooeciopores have not been positively identified.

Remarks. Multifascigera debenensis resembles the *Buskia tabulifera* described by Reuss (1864, p. 64, pl. 8, figs. 1–4) from the German Oligocene but has fewer fascicles per subcolony and a tighter packing of subcolonies. *Buskia* Reuss, 1864 is a junior homonym of *Buskia* Alder, 1857, a Recent ctenostome bryozoan. This new Coralline Crag species is most appropriately referred to *Multifascigera* d'Orbigny, a genus previously recognized only in the Cretaceous. The type species of *Multifascigera*, *M. campicheana* d'Orbigny 1853, has been redescribed by Walter (1972). Assignment of *Multifascigera* to the family Theonoidae is due to the morphological similarity between the subcolonies of this genus and single colonies of *Theonoa*.

Stratigraphical occurrence. The species has been found only in facies A (see facies descriptions below) of the Coralline Crag (Gedgravian) at Ramsholt Cliff.

COLONY GROWTH PATTERNS

The overall shape of the colony is broadly similar in all four species. Colonies are usually spheroidal to oblate spheroidal, less commonly hemispherical or tabular. Colony shape has been quantified in a sample of complete colonies and its variation is illustrated in text-fig. 3 using Zingg plots (modified after Folk 1974). Most colonies have a long axis between about 4 and 8 cm long, although some colonies of *Meandropora aurantium* measure up to 16 cm in diameter.
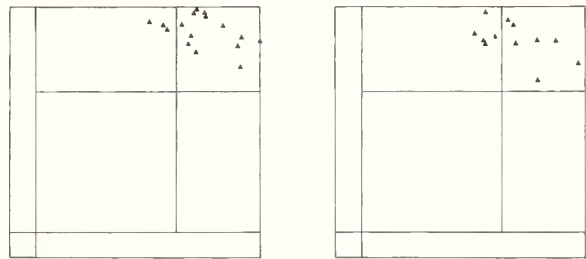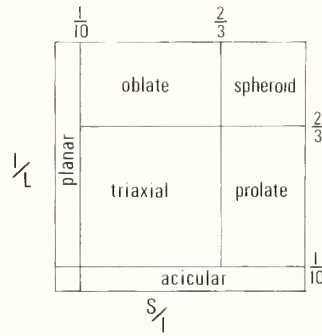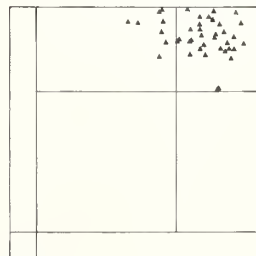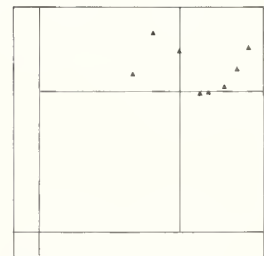

TEXT-FIG. 3. Zingg plots illustrating shape variation among large cyclostome colonies from the Coralline Crag. The upper diagram shows shape nomenclature determined by plotting axial dimension ratios (S = short axis, I = intermediate axis, L = long axis). A, *Meandropora aurantium* (Milne Edwards in Lyell), 16 colonies from Aldeburgh. B, *Meandropora tubipora* (Busk), 12 colonies from Aldeburgh. C, *Blumenbachium globosum* Koenig, 40 colonies from Aldeburgh and Iken. D, *Multifascigera debenensis* sp. nov., 8 colonies from Ramsholt.

The majority of colonies grew radially outwards from an origin situated close to the centre of an encrusting base. A minority of colonies have their origin situated within the core of the colony (see below). In both cases, however, growth was achieved by extension, division, and anastomosis of distinct groups of zooecia comprising subcolonies. This style of colony growth is common to all four species from the Coralline Crag but there are significant differences in the precise pattern
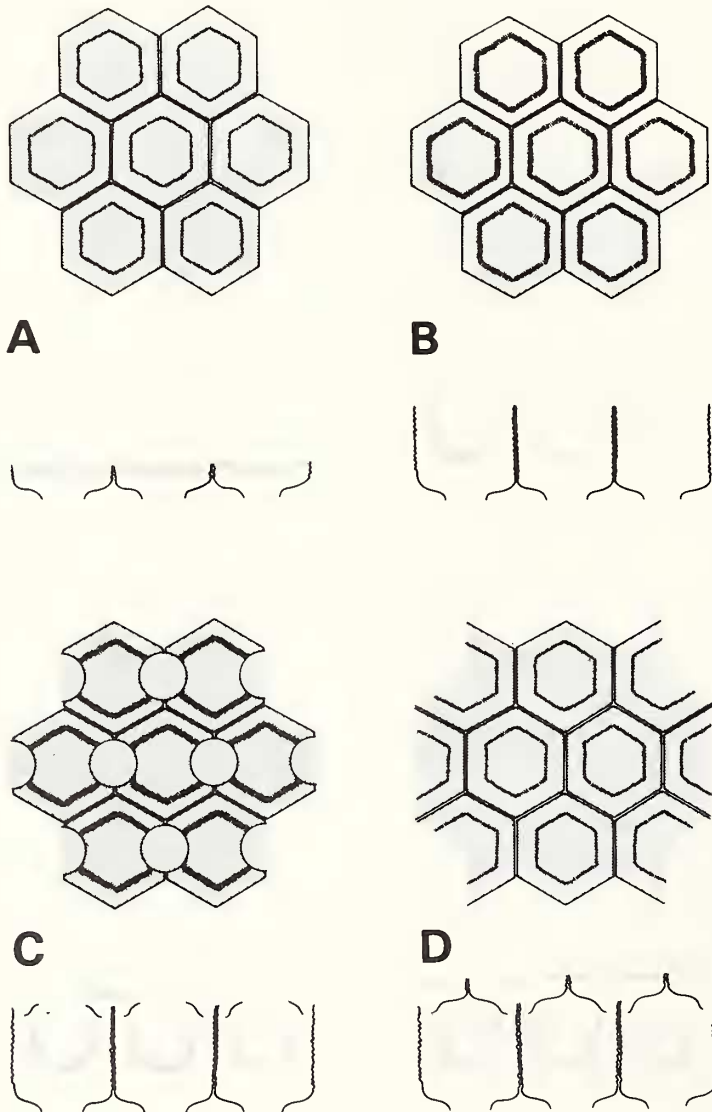
TEXT-FIG. 4. Four stage (A–D) model of colony growth pattern in *Blumenbachium globosum* Koenig. The top diagram for each growth stage shows the colony surface, the bottom diagram is a vertical section. Exterior walls are shown by solid black lines (areas enclosed by exterior walls are subcolonies), inferred hypostegal coelom is stippled, and the steep sides of the ridges around the edges of subcolonies are hatched. Explanation of sequence of events is in the text.

of growth between the species. Colony growth patterns and inferred processes of growth are described below with the aid of simplified diagrams (text-figs. 4, 9–11) depicting geometrically 'ideal' colonies and eliminating zooecial details and incidental irregularities.
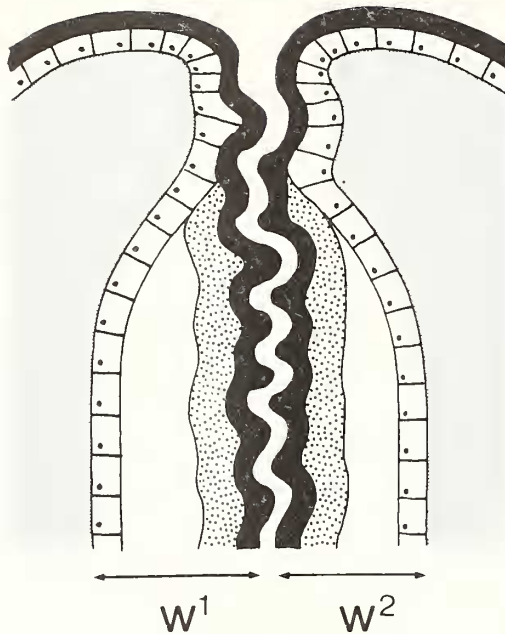
Blumenbachium globosum

Early colony development has not been studied; early growth stages are often not preserved or are difficult to identify in large and complex colonies.

Text-figure 4 is a model illustrating growth in a portion of an idealized mature colony. The initial surface view (text-fig. 4a) shows seven subcolonies, three of which are cut medially by the diagrammatic section. Each subcolony is bounded by a wall inferred to be a calcified exterior wall, i.e. a calcified wall with an external cuticular layer situated at the colony: environment interface (Boardman and Cheetham 1973). Exterior walls of adjacent subcolonies are juxtaposed and interdigitate with one another to form a complex suture (text-fig. 5). A brown layer, probably representing cuticular remnant (intercalary cuticle), is commonly situated between these adjacent calcitic walls. Tavener-Smith (1975, text-fig. 1) has previously illustrated this structure and his diagram implies that the two interdigitating walls were exterior walls rather than interior walls. Interdigitation of exterior walls does not appear to have been described from a cyclostome bryozoan before, although exterior walls bounding individual zooids are well known to interdigitate in certain cheilostome bryozoans (Banta 1977). The probable distribution of soft tissues in the vicinity of subcolony boundaries in *Blumenbachium* is shown in text-fig. 6.

Upper surfaces of subcolonies are composed of open zooecia of polygonal section. The presence of exposed interzooecial walls indicates that these surfaces were probably enveloped beneath hypostegal coelom during colony life (cf. Boardman and Cheetham 1973, fig. 8). They would have been part of a 'common bud' (*sensu* Borg 1926) within which existing zooecia could have been lengthened and new zooecia budded. Each subcolony would have possessed a separate hypostegal coelom extending as far as the exterior wall bounding the subcolony (text-fig. 4a). Small, newly budded zooecia are concentrated in zones immediately adjacent to the subcolony-bounding exterior walls. These walls evidently functioned as sites of zooecial budding (budding laminae), although zooecial buds also arose in smaller numbers elsewhere on the upper surfaces of the subcolonies.

TEXT-FIG. 5. Interdigitating exterior walls bounding *Blumenbachium globosum* Koenig subcolonies. A, thin section, D 52767, ×100. B, S.E.M. photograph of complexly folded wall on the broken edge of a subcolony, D 53128, ×90.

TEXT-FIG. 6. Reconstructed vertical section through the growing edge at the boundary between two contiguous subcolonies of *Blumenbachium globosum* Koenig. Inferred exterior walls bounding the two subcolonies are labelled W^1 and W^2. Each consists of a cuticular layer (solid black), a primary calcified skeletal layer (coarse stipple), a secondary calcified skeletal layer (unshaded), and an epithelial layer (nucleate rectangular cells). Hypostegal coelom is shown by fine stippling. The gap between interdigitating cuticles is exaggerated.

Concentration of zooecial budding and growth close to the peripheries of the subcolonies gave the subcolonies slightly raised edges (text-fig. 4A) which were usually accentuated during subsequent colony growth until they became distinct ridges (text-fig. 4B). Fossils are frequently found with prominent ridges on the colony surface (Pl. 55, fig. 5).

The next stage of growth involved the formation of a new generation of subcolonies on the upper surface of the colony. An initially short and curved length of exterior wall appears to have arisen from the distal ends of interzooecial walls (cf. Taylor 1978, text-fig. 8). Both ends of this wall gradually extended laterally until they joined thus isolating a subcircular patch of zooecia from the surrounding zooecia (text-fig. 4C). Zooecia within this exterior wall constituted a new subcolony (text-fig. 2B). The occurrence of numerous zooecial buds and the thickened zooecial walls within the new subcolonies suggest that this stage of growth was one of rejuvenation. However, intrazooecial fission of the type documented at a comparable position in other stenolaemates (Hillmer, Gautier and McKinney 1975) is not evident in *Blumenbachium*.

Each new subcolony apparently originated within the boundary walls of an established subcolony but in a variety of possible situations including ridge crests, ridge flanks, and depressions at the centres of the subcolonies. Commonly, two closely adjacent new subcolonies situated on either side of a ridge crest coalesced at an early stage in their growth, as in the model colony (text-fig. 4C). New subcolonies attained a low cup-shape by upward and outward growth. Continued growth caused them to overarch subcolonies of the previous generation and eventually to contact adjacent subcolonies. Instead of coalescing on contact, however, the bounding exterior walls of the subcolonies were retained and became interdigitated in the manner described previously (text-fig. 4D). A growth stage equivalent to the first growth stage (text-fig. 4A) had now been reached. Large colonies were constructed by several repetitions of this growth cycle.

The model colony (text-fig. 4) differs from a natural colony in the regularity of its subcolonies. Although subcolonies in fossil *Blumenbachium* are on average six-sided, some subcolonies may have only three sides and others may have eight or more sides. This variability (text-fig. 7) is largely a consequence of irregularity in the location of new subcolonies. Subcolonies are not evenly spaced. An additional geometrical factor precludes the possibility of a spheroidal colony being composed of hexagonal subcolonies. Space cannot be enclosed solely by hexagons (Thompson 1961, p. 157).
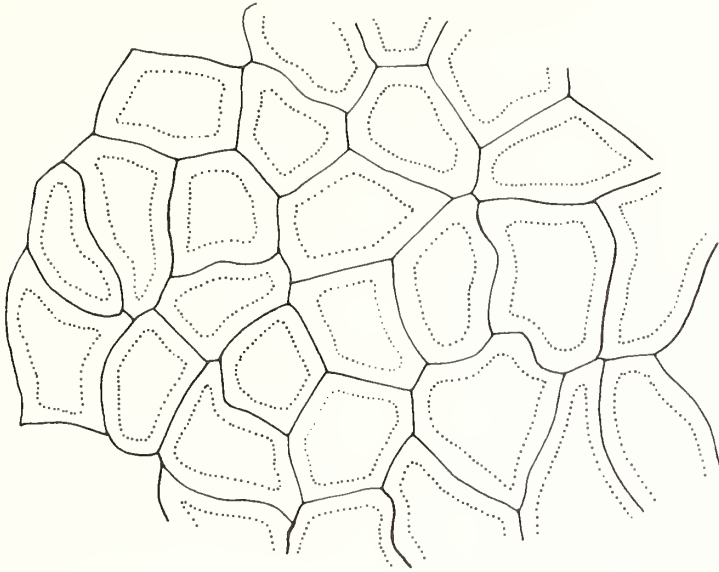
TEXT-FIG. 7. Subcolony shape drawn from the surface of a typical colony of *Blumenbachium globosum* Koenig (cf. text-fig. 4A). Boundaries between subcolonies are shown as solid lines and ridge sides as dotted lines. D 51069, Coralline Crag, Sudbourne, ×4.

Growth in *Blumenbachium* produced a multilayered colony (Pl. 55, fig. 6; Pl. 56, fig. 1) with each concentric layer consisting of a single generation of subcolonies united at their edges. Between the layers is enclosed a considerable volume of void space. Some of the colonies which have been sectioned reveal a variably defined dimorphism in the structure of the concentric layers with alternate layers being composed of relatively low-ridged and high-ridged subcolonies (text-fig. 8).
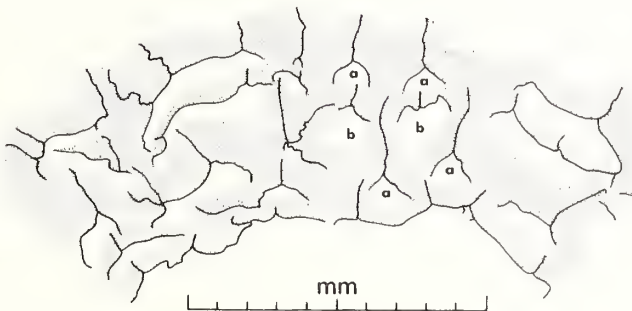
TEXT-FIG. 8. *Blumenbachium globosum* Koenig, D 6905. Drawing of part of a thin section through a colony showing three or four concentric growth cycles (cf. text-fig. 4D). Dimorphism in the growth cycles is well developed right of centre where two alternating types of lacunae are visible: a, lacunae between low subcolonies; b, lacunae between high ridged subcolonies.
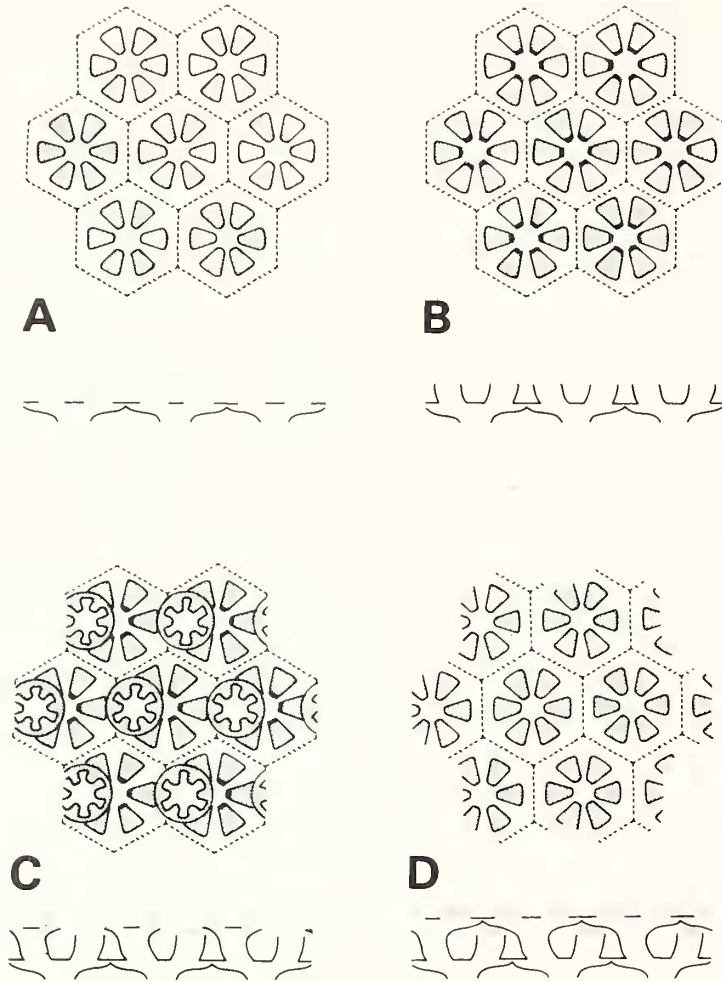
TEXT-FIG. 9. Four stage (A–D) model of colony growth pattern in *Multifascigera debenensis* sp. nov. The top diagram for each growth stage is the surface of the colony, the bottom diagram is a vertical section. Exterior walls (enclosing fascicles and subcolonies) are shown by solid black lines, inferred hypostegal coelom is stippled, anastomoses between subcolonies are dashed, and the steep proximal sides of divergent fascicles are hatched. Full explanation in the text.

Multifascigera debenensis

None of the available colonies preserve early growth stages but comparison with known tubuloporinids of similar form (e.g. *Theonoa*) suggest that *Multifascigera debenensis* colonies may have begun growth as adnate fan-shaped expansions which later became discoidal when lateral lobes of the fan coalesced behind the ancestrula (see Borg 1926). The apertures of zooecia in early parts of colonies may have been isolated from one another, as in *Theonoa*, with later zooecial apertures grouped into fascicles.

Surfaces of large colonies show numerous subhexagonal subcolonies each having a series of radially arranged fascicles (text-fig. 9A). These fascicles are typically four-sided, broaden towards the outer edge of the subcolony, and are surrounded by pseudoporous exterior wall which covers the upper surface of the subcolony between fascicles. Boundaries between adjacent subcolonies are indistinct (dotted in text-fig. 9) and sections show that subcolonies are not separated from one another by exterior walls as in *Blumenbachium*. Interzooecial walls (interior walls) bordering contiguous zooecial apertures are exposed on the upper surfaces of the fascicles. This implies the presence of hypostegal coelom capping each fascicle during colony life. Fascicles were initially extended obliquely upwards by the lengthening of existing zooecia (text-fig. 9B). A minority of fascicles, about one per subcolony, then grew rapidly upwards and outwards to overarch the other fascicles (text-fig. 9C). Each of these fascicles was destined to become a new subcolony within a new generation of subcolonies. Exterior wall was formed over the centre of the upper surface of the incipient subcolonies and in a series of strips radiating outwards from this central area. This exterior wall resulted from the division of interzooecial walls on meeting the outer epithelium covering the hypostegal coelom (see Taylor 1978, text-fig. 8) which capped the original fascicle. The extent of hypostegal coelom was now restricted to a series of strips on the surface of the incipient subcolony. Continued lateral expansion of subcolonies occurred by the extension of existing zooecia and budding of new zooecia on the budding lamina formed by the exterior wall which bounded the original fascicle. Adjacent subcolonies eventually met and coalesced (text-fig. 9D) to form a complete platform or layer across the colony surface. Because the new subcolonies of the model colony are equidistantly spaced, each subcolony attains a hexagonal plan view. However, both the shape of the subcolonies and the number of fascicles per subcolony vary considerably in natural colonies (Pl. 54, fig. 1). Growth of exterior wall on the upper surface of each subcolony in the model colony results in the isolation of six fascicles per subcolony. The model (text-fig. 9D) has now reached a stage equivalent to the first growth stage (text-fig. 9A) although the new subcolonies are not aligned directly above the original subcolonies. Large multilayered colonies were constructed by numerous repetitions of this growth cycle.
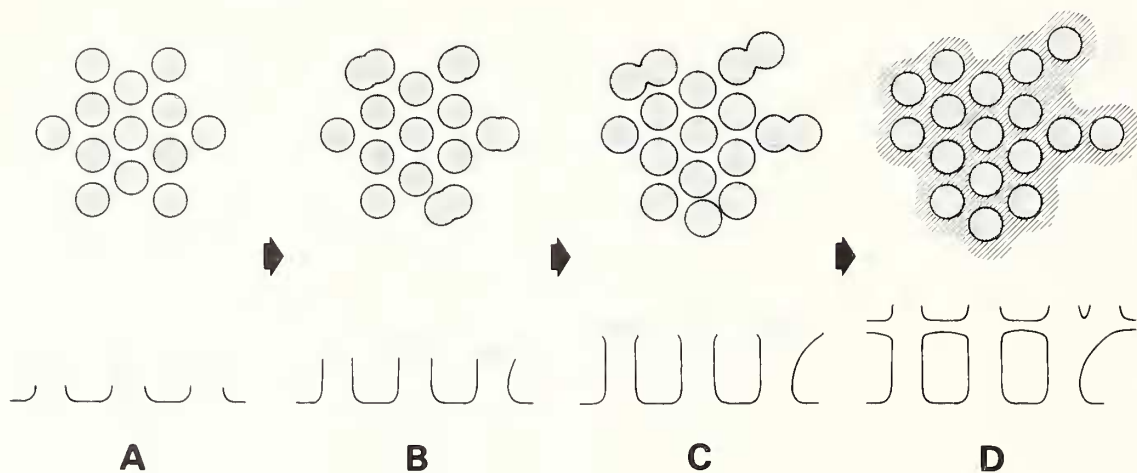
Meandropora tubipora

As in the two previous cyclostome species, colonies of *Meandropora tubipora* are organized into a series of subcolonies. In *Meandropora* these are columnar fascicles (Pl. 55, fig. 2) consisting of elongate zooecia surrounded by a pseudoporous exterior wall. Zooecia open at the tops of the fascicles where the existence of exposed interzooecial walls (interior walls) indicates the presence of a capping hypostegal coelom during life. Each fascicle would have possessed a separate hypostegal coelom which was not confluent with those of other fascicles.

Thirteen fascicles are shown in the surface view of the model colony (text-fig. 10A). Three of the fascicles are cut medially in the section beneath. Upward fascicle growth (text-fig. 10B) was achieved principally by the lengthening of existing zooecia. Budding of new zooecia was subordinate and occurred either by interzooecial wall division within the fascicle or on the budding lamina formed by the exterior wall bounding the fascicle. Colony growth usually involved an increase in the surface area of the colony and necessitated intercalation of new fascicles, formed by fascicle division, if constant fascicle spacing was to be maintained. During their upward growth, fascicles first became elongated along the axis in which division was to occur (text-fig. 10B) and then constricted centrally until they divided into two (text-fig. 10C). The two new fascicles were each bounded by an exterior wall and each would have had its own capping of hypostegal coelom.

A characteristic feature of growth in *M. tubipora* was the regular anastomosis of fascicles. After an increment of upward growth, the fascicles began to expand laterally (text-fig. 10C), apparently by increased zooecial budding on the lamina formed by the fascicle-bounding exterior wall. Eventually adjacent fascicles met and coalesced. Their bounding exterior walls broke down on coalescence suggesting hypostegal coelomic continuity between fascicles and the existence of a single extensive hypostegal coelom over the surface of the colony. Fascicle coalescence gave an

extensive platform of zooecia which is shown to be complete and continuous in the model (text-fig. 10D). In fossil colonies, however, gaps in the platform are common and are a consequence of the failure of certain expanding fascicles to reach adjacent fascicles (Pl. 54, fig. 3). After formation of the platform a new generation of fascicles arose on the surface of the colony (text-fig. 10D). These new fascicles are usually situated almost directly above fascicles of the previous generation. They were isolated from one another by the secretion of exterior walls, in the form of terminal diaphragms (Nye 1968), occluding the orifices of the short zooecia (?kenozooids) occupying the platform between fascicles (Pl. 54, fig. 3). Continued upward growth of the new fascicles resulted in a situation equivalent to that of the first growth stage (cf. text-figs. 10A and 10D). Large colonies were constructed by numerous repetitions of this cycle of growth. When these colonies are fractured open, the platforms formed by fascicle coalescence appear as prominent concentric bands (Pl. 55, fig. 2).

TEXT-FIG. 10. Four stage (A–D) model of colony growth pattern in *Meandropora tubipora* (Busk). The top diagram for each growth stage is the surface of the colony, the bottom diagram is a vertical section. Fascicle-bounding exterior walls as shown by solid black lines, inferred hypostegal coelom (covering the growing edges of fascicles) is stippled, and the platform extending between fascicles is hatched in surface view. Full explanation in the text.

Meandropora aurantium

The growth pattern of *M. aurantium* colonies is similar to that of *M. tubipora* colonies but colonies generally lack abrupt and regular fascicle anastomosis. Consequently, *M. aurantium* colonies do not possess the concentric platforms which characterize *M. tubipora*.

The columnar fascicles of *M. aurantium* are each bounded laterally by pseudoporous exterior wall and zooecia open at the tops of the fascicles where hypostegal coelom existed during life. Extension of fascicles was achieved largely by lengthening existing zooecia, although new zooecia were occasionally budded either by interzooecial wall division within fascicles or on the budding lamina formed by the fascicle-bounding exterior wall. Both division of established fascicles to form new fascicles and anastomosis of fascicles usually proceeded in an irregular manner during upward colony growth, as shown in the model colony (text-fig. 11). Fascicle division followed medial constriction of enlarged fascicles with elliptical cross-sectional shapes; fascicle anastomosis was brought about by the breakdown of exterior walls between converging fascicles. Some colonies (Pl. 56, figs. 6, 7) exhibit concentric bands (up to 1 cm deep) which were the result of periods of extensive fascicle anastomosis and minimization of interfascicular space (Pl. 54, fig. 5).

PALAEOECOLOGY

Coralline Crag facies and bryozoan distribution

The Coralline Crag was deposited during a Pliocene marine transgression over part of east Suffolk. The most conspicuous facies formed during this transgression is a sandwave facies deposited by an offshore sandwave field (facies B). The elongate nature of the outcrop of this facies may be evidence that the facies represents a Pliocene offshore linear sandbank comparable to those off Norfolk at the present time. To the west, on the inferred landward side of this sandwave field is a more silty sublittoral facies (facies A). In some places the sandwave facies is seen to overlie this more nearshore facies. To the north and east on the inferred seaward side of the sandwave facies is a facies of coarse skeletal carbonates (facies C). Nio (1976), in a discussion of the role of marine transgressions in the formation of sandwave complexes, described the sequence of facies which results from increasing water depth. Where water depth is sufficient, strong tidal currents offshore may result in the formation of large sandwaves (sandwave facies). Sandwaves will not develop in shallower sublittoral waters. In deeper offshore waters water depth may be too great and/or currents too weak for the production of large sandwaves. With increasing water depth during the transgression these facies migrate landwards with the more offshore facies overstepping the onshore facies. This facies sequence has been recognized in the Coralline Crag. Each facies has a characteristic lithology and fauna (Balson 1981) which are summarized below.

1. *Facies A.* Bioclastic silty sands were deposited on the landward side of the sandwave facies. This facies is best seen in the Ramsholt area where the sediments show evidence of intense bioturbation which has obliterated any previously existing sedimentary structures. The sediment is generally more poorly sorted and has a higher terrigenous content than that of the sandwave facies indicative of weaker currents and greater proximity to the shoreline. This facies usually contains a rich, diverse, and well-preserved fauna. Large infaunal bivalves (e.g. *Glycymeris*) are common and are frequently articulated indicating minimal reworking of the sediment by currents. Bryozoans are abundant including large irregular celleporiform (see Schopf 1969 for terminology and descriptions of bryozoan growth-forms) cheilostomes which formed substrates for organisms such as the coral *Cryptangia* (Buge 1952; Pouyet 1978). Erect eschariform and adeoniform colonies of *Metrarabdotos* are also common. These bioturbated sediments are overlain by coarser bioclastic sediments showing trough cross-stratification produced by megaripples with amplitudes of approximately 50 cm. The foresets frequently have silt drapes indicating periods of increased fine sediment input which may be related to storm events. Demonstrably *in situ* fauna is much rarer in this upper part of facies A.
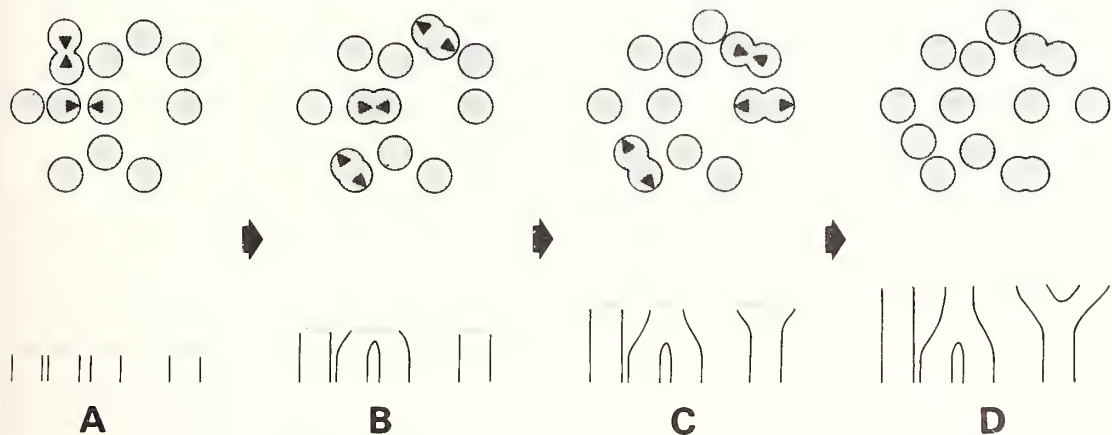
TEXT-FIG. 11. Four stage (A–D) model of colony growth pattern in *Meandropora aurantium* (Milne Edwards in Lyell). The top diagram for each growth stage is the surface of the colony, the bottom diagram is a vertical section. Fascicle-bounding exterior walls are shown by solid black lines and inferred hypostegal coelom (covering the growing edges of fascicles) is stippled. Divergent arrowheads indicate dividing fascicles, convergent arrowheads anastomosing fascicles.

The environment of facies A was evidently one of sheltered inlets, formed by the drowning of a pre-existing topography. The large amount of fine sediment present may be due to a position at the end of a sediment transport path (Balson, in preparation). Deposition was relatively slow allowing extensive bioturbation. As water depth increased, tidal currents became established resulting in an increased coarse sediment input and the formation of megaripples.

Multifascigera debenensis is known exclusively from this facies where it occurs with occasional colonies of *Meandropora aurantium* and poorly preserved ?*M. tubipora. Blumenbachium globosum* is a notable absentee.

2. *Facies B*. The Coralline Crag of the Orford–Sudbourne area is characterized by the presence of large-scale cross-bedding produced by sandwaves of between approximately 1 and 3 m amplitude. The sandwaves were generated by dominantly unidirectional tidal currents flowing to the south-west. The fauna of this sandwave facies which is demonstrably indigenous is sparse and has a low diversity. Bivalve shells tend to be fragmented and abraded. Deposition was probably rapid but sporadic, resulting in well-defined individual foreset laminae. Periods of deposition were characterized by large amounts of bedload transport and reworking of bottom sediments, perhaps during storms. The bioclastic sand of the sandwave facies is consequently well-sorted with the carbonate material comminuted and highly abraded. Environments of this type are not easily colonized by benthos and it is likely that the abraded skeletal fragments, including those of *Meandropora* and *Blumenbachium*, were transported from elsewhere.

3. *Facies C*. This facies formed on the seaward side of the sandwave field and is now exposed in the Aldeburgh area as bioclastic sands with bedding horizontal or dipping at low angles. The sediment is generally coarse skeletal sand with only small quantities of fine or terrigenous sediment grains. The occurrence of occasional silt drapes indicates periodic increased deposition of fine sediment which may be related to storm events. The benthic fauna is both abundant and diverse. Moulds of large, often articulated, aragonitic bivalves may reveal clionid borings and encrustation by bryozoans. Calcitic bivalves such as *Chlamys* may also have an abundant and well-preserved encrusting epifauna which includes serpulids and bryozoans with membraniporiform and celleporiform growth-forms. Other celleporiform colonies are penetrated by narrow cylindrical voids which were probably left after the decomposition of an organic substrate, e.g. a hydroid. Horizontal burrows are locally abundant in this facies. The presence of articulated cellariiform bryozoan colonies is particularly notable. The calcareous internodes of these bryozoans were originally held together by chitinous nodes which would have decayed soon after death (Lagaaij and Gautier 1965). Preservation of articulated internodes implies minimal transportation and rapid burial. It appears that facies C was formed in an environment not influenced by strong currents (cf. sandwave facies) where bedload transportation was less prominent. Prevailing sedimentation rates may have been low, allowing the development of a diverse epifauna and extensive bioturbation between sporadic larger influxes of sediment.

The large cyclostomes reach their greatest abundance in facies C. *Blumenbachium* is particularly numerous and some colonies are penetrated by cylindrical voids in the same way as the celleporiform cheilostomes. Fine-grained sediment settling from suspension on to the surface of the large cyclostomes could be cleared by the powerful extrazooidal feeding currents (Taylor 1979) the bryozoans may have created during life.

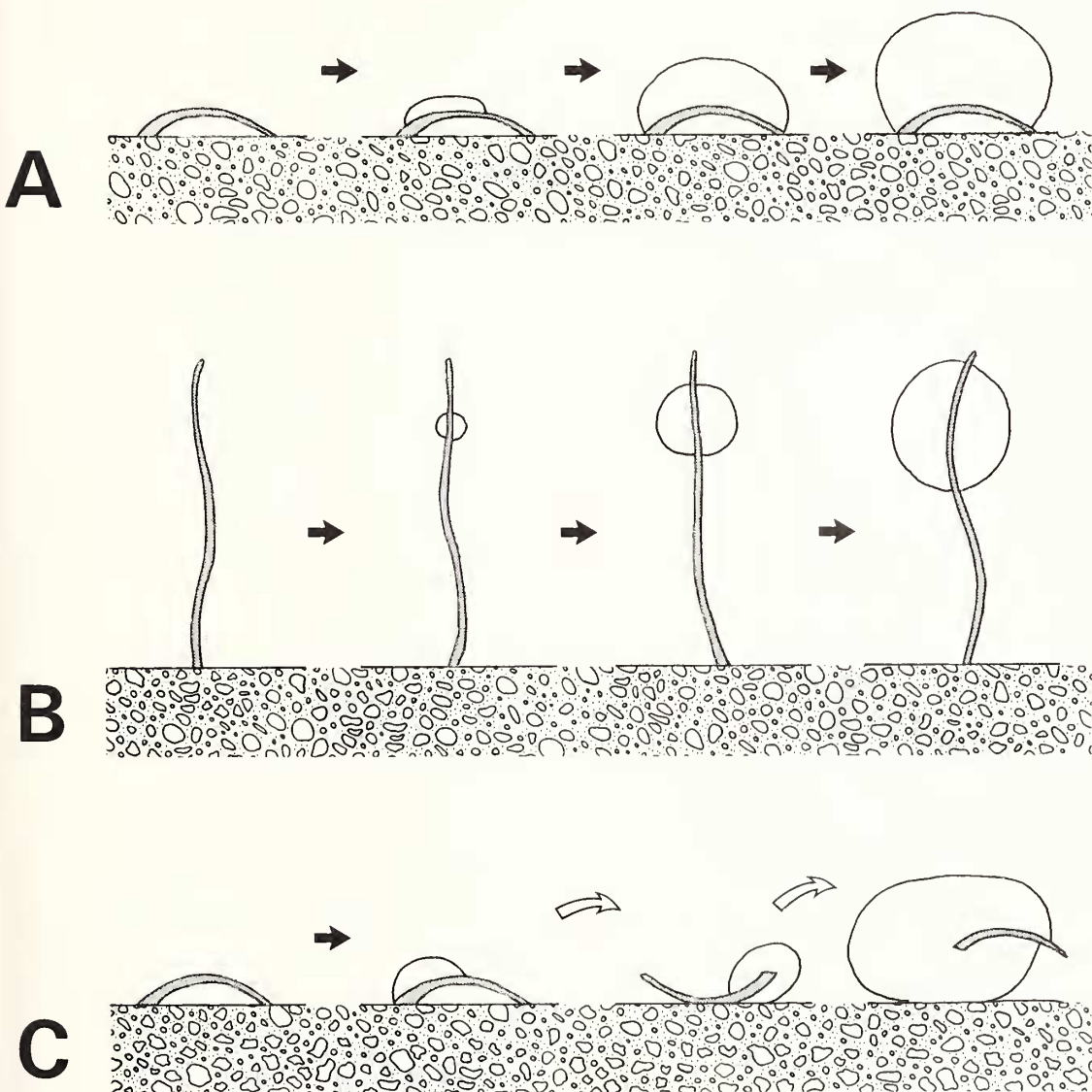## Development of different colony shapes

Three distinct colony types can be recognized among the large cyclostomes on the basis of inferred developmental history (text-fig. 12).

1. *Colonies which had an external basal substrate*. These colonies developed in the conventional manner for a sessile bryozoan (text-fig. 12A). The substrate they encrusted remained comparatively stable on the sediment surface and consequently had a permanent undersurface inaccessible to the bryozoan. Semi-erect bryozoan growth on the upper surface of the substrate gave a mound-like colony with a moderately high sphericity (Pl. 55, fig. 6; Pl. 56, fig. 6).

2. *Colonies which were supported by an unpreserved cylindrical substrate*. In these colonies the original substrate is represented by a narrow cylindrical void which was probably left after the decay of a perishable organic substrate such as a hydroid. This substrate evidently held the colony above the sea-bed (text-fig. 12B) enabling bryozoan growth to proceed equally in all directions and resulting in a colony with a very high sphericity (Pl. 56, fig. 2).

3. *Colonies which enveloped an originally external basal substrate*. Perhaps the most interesting colonies are those which partly (Pl. 56, fig. 7) or totally (Pl. 56, figs. 3, 4) envelope their original substrate of attachment. Their substrate was evidently a mobile skeletal fragment lying on the

sea-bed. Changes in the orientation of the substrate brought different portions of the bryozoan colony into contact with the sediment surface and while these parts undoubtedly ceased to grow, other parts of the colony continued to grow. An originally external basal substrate could only become totally enveloped (text-fig. 12c) by being overturned. Comparable colony forms have been previously described in fossil and living bryozoans (Flor 1972; Rider and Enrico 1979). Morphological and developmental comparisons can also be made with algal rhodoliths (Bosellini and Ginsburg 1971; Focke and Gebelein 1978) and certain colonial corals (Kissling 1973; Glynn 1974)

TEXT-FIG. 12. Development of different colony shapes in large cyclostomes from the Coralline Crag. A, four stages in the development of a colony attached to a substrate (stippled bivalve shell) resting stably on the sea-bed. B, colony supported above the sea-bed by an erect, soft-bodied substrate. C, circumrotatory colony partially enveloping a substrate (bivalve shell) which was overturned.

which have been termed 'circumrotatory'. This term is here applied in a developmental rather than strictly morphological sense to describe bryozoan colonies which were reorientated during their growth. Conversely, colonies which evidently maintained a constant orientation are referred to as non-circumrotatory. Application of a developmental distinction avoids confusion between circum-rotatory colonies and non-circumrotatory colonies whose radial growth was the result of being supported above the sediment surface (colony type B above).

The nature of the substrate may have been a major factor determining whether colonies achieved circumrotatory growth. Bivalve shells appear to have been the commonest substrates colonized by the large cyclostomes. These shells would have formed comparatively stable substrates when orientated in a convex upwards attitude (e.g. Pl. 55, fig. 6). Indeed, many colonies attached to bivalve shell substrates are non-circumrotatory; those which are circumrotatory have a fairly low sphericity because the flat shape of the bivalve is strongly reflected in the shape of the bryozoan colony (e.g. Pl. 56, fig. 7). High sphericity as a result of circumrotatory growth is often seen when the substrate is small, e.g. bryozoan (Pl. 56, figs. 3, 4) and shell fragments. Small substrates were easily overturned and their shape was not strongly reflected in the shape of the bryozoan colony. Other substrates utilized commonly include turritellid gastropods (Pl. 56, fig. 5). Some colonies evidently gained secondary substrates, including fragments of other bryozoans, during their growth. These secondary substrates probably rested on the sea-bed adjacent to the growing bryozoan colony and became overgrown. Some were totally enveloped during subsequent bryozoan growth.

Overturning of circumrotatory colonies

Circumrotatory growth necessitated overturning of the bryozoan colony and its substrate. This could have been achieved in two principal ways: by current action or by mobile benthic animals. Rider and Enrico (1979) and Kissling (1973) believed that currents were largely responsible for overturning the circumrotatory bryozoans and corals they studied whereas Glynn (1974) thought that overturning was accomplished by animals (e.g. fishes and crustaceans) in search of food and possibly shelter. If currents were responsible for overturning the Coralline Crag cyclostomes the attainment of circumrotatory growth should be more closely related to colony size, and thus stability, than is actually evident (but cf. Kobluk, Bottjer and Risk 1977). No examples have been found where an initially circumrotatory colony later became non-circumrotatory as enlargement increased stability. The Coralline Crag cyclostomes also lack the symmetry of internal structure and sphericity of external form which characterizes probable current-overturned circumrotatory bryozoans (e.g. Pedley, in preparation). The apparent restriction of the large cyclostomes to facies A and C where bedload transportation is least evident, further suggests biological overturning. This may have been accomplished by crabs and fishes which are known to have lived sympatrically with the bryozoans (Bell 1897) or by infauna burrowing in the sediment beneath the bryozoan colonies (the biological bulldozers of Thayer 1979).

EXPLANATION OF PLATE 56

Figs. 1, 3-4. *Blumenbachium globosum* Koenig. 1, ellipsoidal colony (probably circumrotatory) with origin close to centre, D 52755, lectotype, 'White Crag', Suffolk, × 1·1. 3-4, part and counterpart of circumrotatory colony totally enveloping a celleporid cheilostome, D 51070, Coralline Crag, Suffolk, × 1·2.

Figs. 2, 6-7. *Meandropora aurantium* (Milne Edwards in Lyell), Coralline Crag. 2, spheroidal colony penetrated by a narrow cylindrical cavity (not visible in photograph) evidently left after decomposition of a substrate which supported the colony above the sea-bed (cf. text-fig. 12B), Sedgwick Museum C 51085, Sudbourne Hall, × 0·75. 6, hemispherical colony (cf. text-fig. 12A) with growth banding, D 52775, Aldeburgh Hall, × 1·1. 7, circumrotatory colony partly enveloping a bivalve shell represented by a curved hollow (cf. text-fig. 12C), D 52766, Aldeburgh Hall, × 1·05.

Fig. 5. *Meandropora tubipora* (Busk), colony attached to a turritellid gastropod, Coralline Crag, Sudbourne, × 0·9.
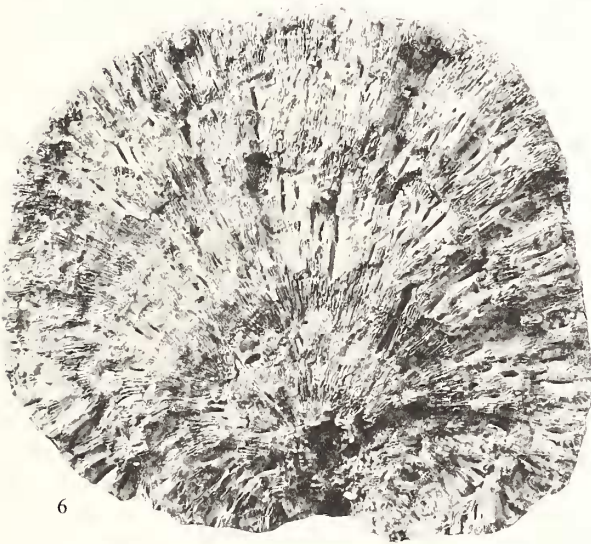
PLATE 56

BALSON and TAYLOR, Pliocene bryozoans
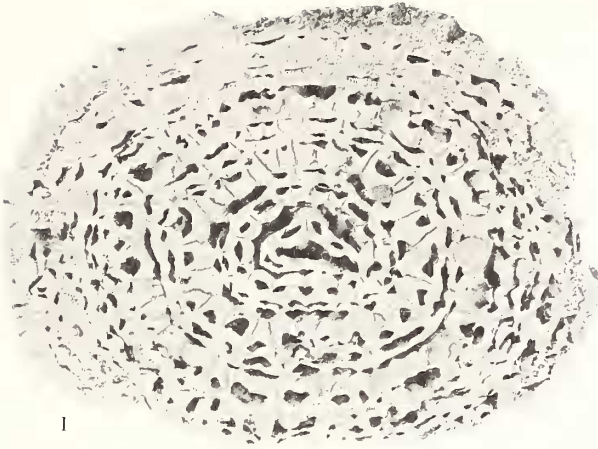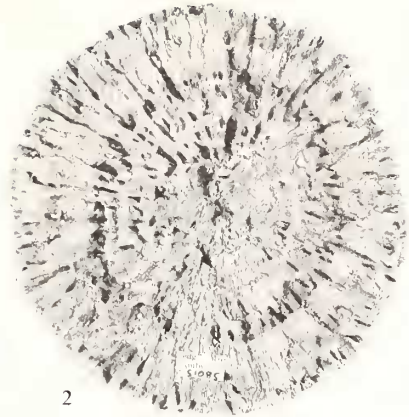
Biotic associates

A conspicuous feature of several colonies is the presence of a large cavity (cf. Glynn 1974) where the earliest-formed parts of the colony and its substrate have been removed (Pl. 55, fig. 1). These cavities truncate skeletal walls and may have a narrow entrance which broadens into a large chamber. Comparable cavities have been described from the Recent by Warme and McHuron (1978) and are also present in living celleporid bryozoans from the Scilly Isles which are the domiciles of crabs (P. J. Hayward, pers. comm. 1978). The Coralline Crag examples may have resulted from the activity of microborers (e.g. algae) and macroborers (e.g. polychaetes) forming an initial cavity and weakened area which could be enlarged by a crab, possibly while the bryozoan was still living. It may be significant that other objects large enough to provide shelters for crabs etc., are rarely preserved in Coralline Crag sediments.

The Coralline Crag cyclostomes often acted as substrates of attachment for various encrusting animals including membraniporiform cheilostomes and serpulid worms (Pl. 55, fig. 5). In several cases the host cyclostome subsequently overgrew these encrusters, thus proving their life association. Serpulids, for example, are often found partly or wholly immersed within colonies of *Blumenbachium globosum*. They evidently colonized the surface of the bryozoan but were covered when a new generation of overarching subcolonies formed. It seems possible that much of this encrusting epifauna became established during periods (?seasonal) of colony dormancy.

DISCUSSION

Subcolonial organization

The four large cyclostomes from the Coralline Crag exhibit a feature commonly found in post-Palaeozoic cyclostomes: division of the colony into a series of subcolonies or cormidia each bounded laterally and/or basally by a calcified exterior wall. This has been described previously in a variety of multilamellar cerioporinids, e.g. Lower Cretaceous *Multicrescis* and *Reptomulticava* (Flor and Hillmer 1970; Hillmer 1971; Hillmer, Gautier and McKinney 1975; Maryanska 1968; Nye and Lemone 1978). It is also known in several tubuloporinids, including fasciculate forms (e.g. *Fasciculipora*, see Malecki 1980) and non-fasciculate forms (e.g. *Cellulipora*, see Buge and Voigt 1972), in melicerititids (*Reptomultelea*), and in rectangulates (e.g. *Lichenopora* spp., see Chapman 1933; Buge 1975). Most of the zooids comprising the cormidia in each of these cyclostomes are skeletally similar and undoubtedly functioned as feeding zooids (autozooids), although some or all cormidia within a colony may also contain non-feeding polymorphs (kenozooids, gonozooids, and, in *Reptomultelea*, mandibulate zooids). In general, cyclostome cormidia appear not to be functional units of the colony in the sense of cheilostome cormidia (Ryland 1979) where the cormidium consists of a group of different polymorphs each performing a different function. Instead, cyclostome cormidia seem to serve as structural units ('building blocks') and probably also as physiological units of the colony.

Cormidia in related bryozoans of the Palaeozoic order Trepostomata have been recently analysed by Anstey and co-workers (Anstey and Delmet 1973; Anstey, Pachut and Prezbindowski 1976; Pachut and Anstey 1979; Podell and Anstey 1979). Trepostome cormidia are centred around protuberances on the colony surface known as monticules. Apart from having a role in filter-feeding (Banta, McKinney and Zimmer 1974; Taylor 1979), monticular cormidia were probably physiological units of the colony. Zooidal budding and other physiological activities seem to have been controlled by morphogens released by zooids at the centre of each monticule. One of the major differences between these monticular cormidia and the cormidia of post-Palaeozoic cyclostomes is that trepostome cormidia do not have well-defined boundaries because they lack the exterior walls which border cyclostome cormidia. The greater skeletal autonomy evident in cyclostome cormidia reflects a greater autonomy of soft parts. Surfaces of trepostome colonies during life were apparently enclosed beneath a common or hypostegal coelom which was colony-wide and continuous across

cormidial boundaries (Boardman 1971). However, the presence of calcified exterior walls at the boundaries of cyclostome cormidia implies that hypostegal coelom did not extend between cormidia; the distal growing edge of the exterior wall marks the limit of hypostegal coelom (e.g. Boardman 1971, fig. 2). Each cyclostome cormidium possessed a separate hypostegal coelom. In the absence of a colony-wide hypostegal coelom, soft tissue connection between cyclostome cormidia could be achieved only via the interzooidal pores (Nielsen and Pedersen 1979) which penetrate interior walls between zooids. These pores probably allowed activities of individual cormidia (e.g. growth) to be co-ordinated in cyclostomes whereas the colony-wide hypostegal coelom and associated membranes may have the necessary intercormidial connections in trepostomes which lack interzooidal pores. Interzooidal pores are infrequently developed in Palaeozoic stenolaemates (cf. ceramoporoid cystoporates and some cyclostomes, see Utgaard 1973, Brood 1975) and their proliferation during the post-Palaeozoic may have paved the way for the evolution of diverse stenolaemates with well-defined cormidia bordered by calcified exterior walls.

The widespread occurrence of exterior wall bounded cormidia in post-Palaeozoic cyclostomes belonging to diverse taxa implies that this type of organization confers adaptive advantages. Subdivision of colonies resulting in decentralization may allow more precise control of zooid activities and responsiveness to environmental heterogeneities both within and between colonies. A further significant advantage may relate to the localization of colony damage. In a large colony with an extensive colony-wide hypostegal coelom, coelomic rupturing may have a widespread effect, disrupting both feeding and growth until repair could be completed. In a large colony with many small cormidial hypostegal coeloms, coelomic rupturing may be localized to a single coelom leaving most of the colony unaffected. This would have been particularly important to those Coralline Crag cyclostomes which seem to have been regularly overturned.

The large cyclostomes of the Coralline Crag evidently lived attached to a wide variety of substrates. While some colonies were supported above the sea-bed by soft-bodied organisms others utilized shells, varying in shape, size, and stability, resting on the sea-bed. This indicates a relative lack of habitat selection by the settling bryozoan larvae and would have meant that developing colonies may have encountered a variety of different small-scale environmental conditions. Like many plants (Bradshaw 1965), colonial animals can respond to habitat variations by phenotypic plasticity in growth. The large cyclostomes from the Coralline Crag had the capacity to mediate a plastic response not only at zooidal level but also at the additional hierarchical level of the subcolony.

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